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GALLS AND INSECTS PRODUCING THEM.*

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PART VI. FLOWER AND FRUIT GALLS.

Galls affecting flowers and fruits are not so abundant as those affecting leaves, but in many cases the insect which produces flower or fruit galls also produces leaf galls. No sharp line of distinction can be drawn between flower and fruit galls, since the gall may form and mature without indication of fruit or may form in the flower and mature as the fruit develops. Thus far I have collected five species of flower and fruit galls representing three orders of insects.

1. GALLS OF THE ACARINA.

Phytoptus sp.—on Euphorbia corallata L. (Figures 70; 71a, b; 72a, b). This mite produces galls on both leaf and flower. The structure of the gall is the same in both cases and is identical with Phytoptus galls, previously described in Part I, (Figures 8–11). All my specimens of this gall were well advanced. The structure of the leaf of E. corallata (Fig. 70) is typical. When attacked by the Phytoptus the leaf becomes very much modified by thickenings, ridges and convolutions (Figures 71a, b). The palisade cells divide so that it is impossible to distinguish them from the mesophyll, and the intercellular spaces are obliterated as the result of the rapid cell division. The new cells are small and very rich in protoplasm, but gradually become filled with tannin as the gall approaches maturity. The tannin first forms in the outer and most exposed cells of the gall while the inner layers of cells retain their protoplasm very late. The Phytoptus restricts its attacks to these inner and more protected parts. From a study of these galls it is apparent that the Phytoptus is not working on

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all parts of the gall at the same time, but gradually moves outward over the surface of the leaf, thus increasing the size of the gall and drawing its food supply from the newer part thus formed.

When the attack is made upon the flower we have a mass of distorted tissue which is structurally the same as that produced in the leaf gall (Figures 72a, b). The floral envelopes are the first to suffer from the attack, the ovary with its contents is the next greatest sufferer, while the stamens are frequently unaffected. It is evident that the attack upon the flower must be made very early in order to cause complete destruction. Very frequently the floral envelopes will be very much deformed and the ovary and the stamens very slightly affected. In other cases the ovary will be very much enlarged and its chambers practically obliterated. It is evident that the attack upon the ovary must be made very early to produce a great deformity. The partial immunity of the stamens is probably due to their being very nearly mature before the opening of the bud.

2. GALLS OF CECIDOMYIA.

Cecidomyia anthophila O. S.—on Solidago canadense L. (Figs. 73a, b), makes the attack early and completely prevents the opening of the bud. The gall is in the form of a hollow cone. The transformation is so complete that the location is the only evidence that the gall is produced from a flower bud. A section of the gall shows the nutrient layers of the cells next to the larval chambers, large parenchyma cells near the outer epidermis, and a number of rather weak fibro-vascular bundles.

Cecidomyia sp.—on Ratibida pinnata Barnhart (Figs. 74a, b, c). The entire bud is transformed into a gall with the larva in a chamber in what was originally the ovary. All the floral parts have become modified and united to form the gall. A section of the gall (Fig. 74c) shows that the cells are more uniform in size than in the preceding galls and that the fibro-vascular bundles are practically obliterated.

Cecidomyia sp.—on Prunus virginiana L. (Figs. 75a, b). My specimens of this gall were mature. I am unable to say at what time the gall originates, but it reaches its maturity with the fruit. The gall is somewhat larger than the fruit, but otherwise resembles it closely. The larva makes its exit through an opening at one side of the stem. The larval chamber is very large, thus giving the gall a bladder-like character. The cuticle is well developed and the parenchyma cells below it are very large, while the cells next to the larval chamber are much smaller. Weak fibro-vascular bundles are also present. The wall of the gall (Fig. 75b) is much thicker than the wall of the fruit at this time (Fig. 75a), and parenchyma cells are much larger. The characteristic stone (sclerenchyma) of the fruit is never developed in the gall.

3. GALLS OF LEPIDOPTERA.

I gathered a number of Lepidopterous galls on Rudbeckia laciniata L. which I was unable to determine. These galls occur on both leaf and flower and are very large and fleshy. In fact they were so fleshy and juicy that it was very difficult to secure sections. The parenchyma cells were very large, and small fibro-vascular bundles were numerous. The larval chambers were numerous and each contained a single larva or pupa. In my specimens the larvae were far advanced, many of them in the pupa stage, but the cells next to the chambers were very rich in food supply.

PART VII. ROOT GALLS.

Amphibolips radicola Ashm. (Figs. 76a, b).—on Quercus alba L. was the only root gall that I collected. The galls were borne just under the surface of the ground at about the point of transition from stem to root. They were produced in great numbers and so closely packed together as to assume the shape of figs. Those nearest the surface of the ground and therefore slightly exposed to the light were of a rich, red color, while those deeper in the ground were almost white, slightly tinged with yellow. Each gall contained from one to five larval chambers. The younger galls showed four zones well defined (Fig. 76a). The inner or nutritive zone was thick and the cells contained abundance of protoplasm. The protective zone was thin and the cells fibrous in character rather than sclerenchymatous. The parenchyma zone was thick and composed of large parenchyma cells. The epidermal zone was relatively thick and the cells firm. As the insects approach maturity the nutritive and protective zones are entirely destroyed (Fig. 76b). The insect eventually makes its escape through an opening in the side of the gall.

PART VIII. HISTOLOGY OF GALLS.

Many of the histological characters of galls have been referred to in the preceding parts. This part has been introduced at this time for the purpose of adding a few additional facts which were not clear at the time of the writing of the preceding parts.

A. Internal Structures.

1. GALLS OF ACARINA.

These galls have been sufficiently discussed and need very little attention at this time. In general these galls may be thrown into three groups: (1) Those galls in which there is very little distortion, but a modification of the epidermis, as in the case of the Phytoptus on the beech; (2) Convolutions of the parts as in the case of P. ulmi (Fig. 8), P. abnormis (Figs. 9, 44), P. quad-

ripes (Figs. 10, 43), and P. acericola (Figs. 11, 45). These convolutions result in the formation of a more or less well defined cavity, and trichomes are developed in great abundance in the younger stages; (3) Thickening of the parts which become covered with an abundant growth of trichomes as in the case of E. anomalum (Figs. 47, 48).

The Phytoptus galls show two fairly well-defined zones, the outer made up of rather large cells and the inner of much smaller cells, which are very rich in protoplasm and which supply nourishment for the young animal (Fig. 77). As the galls approach maturity the protoplasm disappears, first from the outermost cells and lastly from the cells on the inner surface. As the protoplasm disappears the tannin accumulates in great abundance (Fig. 78).

2. GALLS OF THE APHIDIDAE.

Many of the Aphididae galls produce trichomes which soon disappear. At first all the cells contain protoplasm and divide rapidly, but as the galls approach maturity the tannin increases in abundance.

Schizoneura americana Riley (Fig. 12), Colopha ulmicola Fitch (Fig. 13), and Hormaphis hamamelis Fitch (Fig. 15) have been considered in Part I.

In Pemphigus populi-transversus (Figs. 55, 56) and P. p.-caulis (Figs. 57, 58) the thickness of the walls of the galls is much greater than any other members of this family and the cells are more uniform in character. These galls are especially well supplied with fibro-vasular bundles and are very dense.

In P. vagabundus (Fig. 112) we have a gall in which many of the cells are elongated similar to C. ulmicola and H. hamamelis. Its close structural resemblance to C. ulmicola and H. hamamelis and unlikeness to P. p.-transversus and P. p.-caulis is due to the fact that P. vagabundus, C. ulmicola, and H. hamamelis are formed on the blades of the leaves, while P. p.-transversus and P. p.-caulis are formed on the petioles which are made up largely of fibro-vascular tissue. My specimens of these galls were mature, and I am therefore unable to say anything concerning their early stages.

In the Phylloxera galls all the cells are at first rich in protoplasm and the tannin does not form in abundance until very late. The two zones are fairly prominent. In P. c.-caulus Fitch on H. ovata, a gall which forms on both blade and petiole of the leaf and also on young stems large intercellular spaces are formed near the surface.

3. GALLS OF PSYLLIDAE.

Pachypsylla c.-mamma Riley has been described in Part V (Figs. 59, 60).

4. GALLS OF CECIDOMYIA.

These galls have been described in Part I (Figs. 22, 23, 24), in Part V (Figs. 61, 62, 63), in Part VI (Figs. 73, 74, 75), and in the Appendix (Figs. 114–119). In these galls the two zones are usually fairly well defined, but the galls of this genus are so different in character that it is difficult to give a definite description. The time for the formation of the tannin is variable, but it is usually produced late and in great abundance.

5. GALLS OF THE CYNIPIDAE.

All these galls are very similar. The majority show the four zones and in most cases these zones are well defined. The outer zone is the epidermal which will be described later (Figs. 84–91). The second is the parenchyma zone; the third is the protective zone made up largely of sclerenchyma, and the fourth or innermost is the nutritive zone. In many cases the second and third zones become partially or entirely separated. This separation, however, is not between the second and third zones as previously stated by me in Parts I and V, and by Fockeu, but rather a separation of the tissues of the second or parenchyma zone, the greater part of this zone clinging to the epidermal zone and a few cells remaining attached to the protective zone.

Diastrophus siminis Bassett (Figs. 66–69) has been described in Part V. The four zones are distinct and each shows the character previously referred to.

Diastrophus nebulosus O. S., described in the Appendix (Figs. 129a, b), is a stem gall in which the zones are well defined, the protective zone being especially well developed. Each zone shows the characters previously referred to.

In Amphibolips confluentus Harris (Figs. 121a, b, c) the first and second zones are well developed, but the distinction between the third and fourth is not so pronounced.

In Amphibolips inanis O. S. (Fig. 28) the four zones are well defined. In the young gall (Fig. 79) the cells of the nutritive zones are very rich in protoplasm and there is very little or no distinction between the nutritive and the protective zone, but as the galls approach maturity the cells of the protective zone become very thick and are soon converted into sclerenchyma (Fig. 80).

In Callirhytis papillatus O. S. we have the four zones well defined (Fig. 30). As the gall approaches maturity the cells of the nutritive zone lose their protoplasmic contents and become very much shriveled, the protective zone is made up usually of only two or three layers of cells. Next to the protective zone are two or three layers of cells which are in reality a part of the parenchyma zone. The large intercellular spaces formed in this

zone are bridged by long unicellular threads, but no fibro-vascular bundles (Fig. 81)

Dryophanta palustris O. S. galls show the four zones well defined (Figs. 29, 65). When mature the contents of the cells of the nutritive zone has been entirely used by the insect. The protective zone consists of only two or three layers of sclerenchyma cells, to which are attached a few cells of the parenchyma zone (Fig. 82).

Andricus petiolicola Bassett (Fig. 124) produce a very hard petiole or mid-rib gall which shows the four zones well defined. There is no separation between the second and third zones. The nutritive zone is at first very prominent, but it is reduced as the gall approaches maturity. The protective zone developes its sclerenchyma character rather late (Fig. 83) and gradually merges into the two adjacent zones.

B. Epidermal Structures.

The epidermal cells vary in the size and in the thickness of the cell walls. The galls may be smooth, pubescent or covered with spiny structures. The amount of pubescence depends somewhat on the natural pubesence of the host plant. Galls on such smooth plants as Populus deltoides Marsh show very few and very small trichomes, while galls on plants that are naturally pubescent are likely to be pubescent. These trichomes vary in shape and general character and are very prominent when the gall is young. As the gall approaches maturity the trichomes usually disappear. When these trichomes drop off their place of former attachment is marked by a small mass of small cells, usually containing tannin and from which imperfect rows of cells seem to radiate (Figs. 84–90).

1. GALLS OF CYNIPIDAE.

Dryophanta palustris O. S. is very pubescent when young (Fig. 84a). In the mature gall the cells are much larger, the trichomes have disappeared and their point of attachment is made visible by the accumulation of tannin (Fig. 84b).

All my specimens of Amphibolips inanis O. S. were fully developed, but the points where the trichomes had evidently been attached were very prominent (Fig. 85). These points are the large, black spots so prominent on these large bladdery galls.

In Diastrophus siminis Bassett the trichomes are very large (Fig. 86) and drop off very readily.

In Diastrophus potentillae Bassett the trichomes are very numerous and each is at the apex of a very small elevation (Fig. 87). Examination of the epidermis of Acraspis erinacei Walsh show that its spines were due to similar but much more prominent elevations.

2. GALLS OF THE APHIDIDAE.

Galls belonging to this family are usually less pubescent than those belonging to the Cynipidae. The trichomes are usually much shorter and frequently less numerous. Each trichome is usually made up of a single cell (Fig. 88). The place where these trichomes were attached is marked by an accumulation of tannin, the same as in the Cynipidous galls (Figs. 89, 90).

Examination of the galls of the Phylloxera spinosa Shimer show that the spines were due to the same cause as in the Cynipidous galls (Fig. 87).

Galls of Pemphigus p.-transversus Riley (Fig. 91) and P. p.-caulis Fitch were perfectly smooth, but the cell walls were much thicker than in any other galls studied.

CONCLUSION.

1. The inner layer of cells (i. e., those next to the larva) are always supplied with nutriment until the insect is mature.
2. The development of the other layers of cells is for the protection of the larvae. These protective devices reach their highest development in the Cynipidous galls.
3. In the very young galls there is usually little or no distinction between the nutritive and protective zones. The time of the differentiation of the protective zones varies in different species.
4. The fibro-vascular bundles are most prominent in galls on the petiole and mid-rib.
5. Most galls are covered with trichomes which disappear as the galls approach maturity. The number of trichomes is variable in proportion to the pubescence of the host plant.
6. Spines are due to elevations composed almost entirely of epidermal cells.

PART IX. OVIPOSITORS AND MOUTHPARTS.

One of the most prominent questions concerning the formation of galls which presents itself to the students of entomology and botany and even to the most casual observer, is the exciting factor in gall production. Is the stimulus from the ovipositor or mouth-parts? Is it mechanical or chemical? The author believing that the logical method of solving this problem was to first make a careful study of the morphology and development of galls has published the preceding parts of this paper. The author does not claim to have found a complete solution of the problem, but is hopeful that some of the facts stated in this series of papers may lead to more thorough and satisfactory studies of the problem. The problem presents many difficulties; the parasites and inquilines which are usually present are frequently difficult to distinguish from the real gall-maker; this is especially true when the study is confined to the larvae. In the following studies the author is reasonably certain that the determinations are correct.

OVIPOSITORS.

Gall-making insects deposit their eggs by two methods, either on the surface of the plant or within the tissues. Those insects which deposit their eggs on the surface usually have mouthparts developed for sucking, while those which deposit their eggs within the tissues usually have mouthparts developed for biting. Those which deposit their eggs on the surface of the plant are the Acarina, the Hemiptera, and the Diptera. Those which deposit their eggs within the tissues are the Hymenoptera and the Lepidoptera. In this paper we have made a careful study of the ovipositors of Cecidomyia gleditsiae, of Nematus sp———, Dryophanta palustris, Amphibolips radicola, Andricus cornigerous, A. seminator, and Rhodites radicum. A number of others were examined, but because of the uncertainty as to determination are not figured.

The Cecidomyia ovipositor (Fig. 92) is not suited to puncturing tissues. The gall is never formed until after the hatching of the larva. In this case it is evident that the stimulus, whether mechanical or chemical, is produced by the larva.

Insects belonging to the genus Nematus deposit their eggs either on the surface of the plant or in slits made by the ovipositor (Figs. 93a, b). It is said that the galls are formed from these wounds before the larva escapes from the egg, and in these cases it is claimed that the irritating cause is a drop of fluid secreted by the parent insect. Westwood claims that the egg increasing in size is a result of imbibing sap from the wound in the plant. It is well known that the eggs of some insects increase in size as a result of the growth of the embryo within the egg. I have so far been unable to make any satisfactory observations upon the Nematus galls, but it is probable that the eggs increase in size from the growth of the embryos and not as a result of the absorption of plant sap. It is also possible that the gall may be the result of the mechanical irritation of the ovipositor or the enlargement of the egg or both. The wound caused by the ovipositor of the Nematus is very much more severe than the wounds caused by the ovipositors of the Cynipidous insects.

Adler, after a careful observation on Nematus Vallisnierii, says: "This fly, which is armed with a finely serrated terebra, cuts into the tender leaves of the end of the shoot of the Salix amygdalina, and inserts her egg into the open wound, frequently placing several in the same leaf. At the same time the glandular secretion flows into the wounded leaf. A few hours after this injury the leaf surface presents an altered appearance, and new cell formation begins freely, leading to a thickening of the surrounding leaf surface. After the lapse of about fourteen days the green and red-shaped gall is fully grown. If it be now

opened the egg can still be seen lying within the cavity. The embryonic development is as yet unfinished and three weeks elapse before the larva emerges from the egg to find around it the material prepared for its nutriment. In this case the wound caused by the fly is the immediate exciting cause of cell activity, and leads to gall formation."

M. W. Beyerinck, in a paper regarding the growth of the gall of Nematus caprea on Salix amygdalina holds a similar view. I have not seen this paper, but an abstract* of it says: "The production of the gall is undoubtedly due to the matter secreted by the poison gland, which is, consequently, homologous with the poison of Hymenoptera aculeata; when the insect does not deposit an egg in the wound which it makes, the quantity of albuminous matter poured into the vesicle is always less than when an egg is deposited; by careful observation it is possible to assure oneself that the size of the gall is always proportional to the size of the wound and the quantity of albuminoid matter introduced. By an experiment in which a deposited egg was punctured by a fine needle, it was shown that the gall is due to the parent and not to the egg; but, of course, in such a case the gall remains small; neither the egg nor the larva are necessary for its production, though their presence exercises a certain influence on the regularity of their development."

The ovipositors of the Cynipidae vary in length and in the amount of coiling within the abdomen. All present the same general characters. So far I have been unable to detect any relationship between the length and character of the ovipositors and the location and complexity of the galls (Figs. 94 to 98). Adler claims that the egg is always deposited in or near the Cambium layer of the plant. I am inclined to accept this statement, but have made no special effort to verify it. If Adler's observations are correct the length of the ovipositor would be associated not with the depth of the Cambium from the surface of that part of the mature plant affected, but with the location of the Cambium at the time of oviposition and with the difficulties which the insect would experience in forcing the ovipositor to the desired point.

Oviposition usually occurs before the buds are open, and the eggs may be placed in three positions (1) in the stem, as in the case of Rhodites radicum O. S., R. globulus Beut., Andricus cornigerous O. S.; (2) in the apex of the incipient stem as in Andricus clavula Bassett, and Holcaspis globulus Fitch; or (3) in the leaves of the bud as in Rhodites bicolor Harris, Amphibolips confluentus Harris, A. inanis O. S., A. ilicifoliae Bassett, Neuroterus irregularis O. S., A. seminator, Callirhytis tumifica

*Jour. Roy. Micr. Soc., 1887, p. 746.

O. S., Holcaspis centricola O. S., Dryophanta palustris O. S., and Callirhytis papillatus O. S. In these cases it is evident that the force necessary to penetrate the bud may be as great or even greater than the force necessary to penetrate a stem. Adler's observations demonstrate that great force is used to penetrate the buds and reach the desired point for depositing the eggs.

Beyerinck has demonstrated that the fluid ejected by the ovipositor of the Cynipidae is very different from the fluid ejected from other Hymenopterous insects; that it is without taste or smell and does not irritate when injected under the skin. Adler has demonstrated that this fluid cannot be considered as the stimulus to gall production. It is probable that it may serve to attach the eggs, or as an antiseptic, or as a seal for the wound.

Since the gall does not form until after the hatching of the larva it is evident that oviposition does not furnish the stimulus unless it may be that there is cell division but no swelling of the plant tissues previous to the hatching of the larva. The author has made no observations upon this point. Adler, in discussing this question, says, in regard to Trigonaspis: "This fly pricks the leaf in May, but months pass before any trace of gall formation can be seen. It has tolerably strong ovipositor with which it cuts into the veins of the leaf, and in this way a distinct mark is left wherever an egg has been inserted. Guided by these marks it is easy to find the egg, but it is not until September that the larva leaves the egg, and then gall formation begins."

MOUTHPARTS.

Since oviposition does not give an explanation of the stimulus causing the formation of the gall it is necessary for us to turn our attention to the mouthparts.

For convenience the insects may now be divided into two groups, those with mouthparts for sucking, which make their attacks upon the outside, and those with mouthparts for biting, which make their attacks from the inside. Under the former are included the Acarina, the Hemiptera and the Diptera; under the latter are included the Lepidoptera and the Hymenoptera.

1. HEMIPTERA.

The Hemipterous insects which produce galls may be placed in the following order, with reference to the complexity of their galls, beginning with the lowest: Schizoneura, Colopha, Hormaphis, Phylloxera, Pemphigus and Pachypsylla. Mouthparts of the following were carefully examined: Schizoneura americana Riley, Colopha ulmicola Fitch (Fig. 99), Hormaphis hamamelis Fitch, Phylloxera carya-fallax Riley, P. c.-globuli Walsh, P. c.-spinosa Shimer, P. vastatrix Planchon, Pemphigus populitransversus Riley, P. p.-caulis Fitch, P. vagabundus Walsh,

Pachypsylla celtidis mamma Riley (Figs. 100a, b), and P. c.-gemma Riley.

The study of these mouthparts gave no new anatomical facts. The different genera showed considerable variation as to length of beak and setae. In general it may be said that the setae tend to increase in the distance they may be protruded beyond the tip of the beak as the galls approach complexity. This, however, cannot be considered an exact rule, since the S. americana, C. ulmicola and H. hamamelis have setae of practically the same length, although the gall produced by S. americana is much simpler than the galls produced by either C. ulmicola and H. hamamelis (Part I, Figs. 12, 13 and 15). It was impossible to make exact measurements of the distance the setae protruded beyond the tip of the beak, since it was impossible to tell whether the setae were fully extended or partially retracted. The above conclusions were reached after the examination of a large number of specimens.

So far as I have been able to determine the insects do not remain attached to any one point for a great length of time. The P. c.-mamma (Figs. 100a, b) has a gall of the greatest complexity, and the insect has setae which protrude farther beyond the point of the beak than any other examined; a large number of these galls were opened and the position of the insect noted. The insect was never found attached and apparently had no definite point of attack.

The preceding observations emphasize Conclusions 6 and 8 of Part I and a statement in the first of Part V. That is, the modification of the plant tissue to form the gall is purely mechanical, being a continuous effort on the part of the plant to heal the wound produced by the repeated puncturing of the cells by the insect. When a branch is cut from a tree a growth is produced which tends to cover the wound. In this case a single wound and a single stimulus which is purely mechanical but which produces rapid growth for the purpose of covering the wound. In the case of Aphididae and the Psyllidae galls the wounds are more slight but repeated rapidly, the stimulus is mechanical and the growth rapid, tending to cover the injury.

It is possible that the setae of the various genera may stimulate different tissues and thus cause galls of varying complexity, but upon this question I am not ready to give a definite statement.

2. DIPTERA.

The Cecidomyid galls occur upon a greater variety of hosts than any other group of galls, and as previously stated in Part V, show by far the greatest variation in structural characters and the smallest number of typical characters.

The mouthparts of a number of larvae were examined (Figs. 101, 102), and all were practically the same; salivary or other gland structures could not be demonstrated.

I am inclined to believe that the Cecidomyid galls are due to purely mechanical stimuli and that the great variations are due to the different tissues upon which the larvae feed.

Mr. W. A. Cannon,* in discussing a Cecidomyid gall on the Monterey pine, says that the "larvae take their food only by absorption through the surface of the body," also that "there is no indication that the hypertrophy is either caused or affected by any substance deposited with the eggs."

3. HYMENOPTERA.

We now come to the galls of greatest complexity and also to those with which we have the greatest difficulty. These galls are so very generally infested with parasites and inquilines that it is difficult to decide which larva is the true gall producer.

A careful study of these shows that the insects have a very strong pair of mandibles (Figs. 103 to 108), each working upon two pivotal points. Some of these mandibles appear to have an opening at the tip (Figs. 104, 105), and some showed what appeared to be sacs or glands at the base (Figs. 104, 106b). In one case at least (Fig. 104) these glandular sacs appeared to be connected with the opening. The question that naturally presents itself is, are these openings for the purpose of pouring out a fluid or are they suctorial as in the case of Chrysopa and other families? In only two species was it possible to demonstrate these structures. Some light is thrown upon this by Part VIII, in which it was shown that the cell walls of the inner or nutritive zones were not destroyed, but that the contents of the cells were removed, causing them to shrivel.

The teeth of the mandibles are never on the same plane and the mandibles become more and more chitinous as the larvae approach maturity. The strength of the mandibles appears to depend upon the density of the tissue through which the insect works its way to the outside. In A. inanis (104) and A. confluentus (Fig. 105) the strength of the mandibles is practically the same and the character of the galls very similar. In D. siminis (Figs. 106a, b) the mandibles are stronger and the tissues of the gall correspondingly denser. C. petiolicola (Fig. 103) is by far the strongest of those studied, and the tissues through which the insect must work its way the densest of the leaf galls (Fig. 124).

A study was made of the larvae from galls of C. papillatus. This is a small, rather dense leaf gall. Larvae of two species

*Cannon, W. A. "The Gall of the Monterey Pine." *The American Naturalist*, Vol. XXXIV, No. 406 (Oct., 1900), p. 801.

were found (Figs. 107, 108). A careful study of the mouthparts lead me to consider No. 107 as a true gallmaker and No. 108 as a parasite. The mouthparts of the one which I consider a true gallmaker were as strong as those of C. petiolicola (Fig. 103). The mandibles of the parasite (108) were equally strong and showed what appeared to be rudimentary gland structures.

Holcaspis globulus Fitch was the only bud (i. e., incipient stem gall, Part III, Fig. 34) gall examined. In the young larvae the mouthparts are weak, but as the larvae approach maturity the mandibles become very strong (Fig. 109) and well fitted to cut the opening for the escape of the insect. However, the mouthparts were not so strong as in the case of C. petiolicola, but the gall of H. globulus is not so dense as the gall of C. petiolicola.

The mouthparts of Nematus pomum Walsh (Fig. 110) were very similar to those of the Cynipidae. I am not inclined to consider the apparently glandular-like structure observed in a few species of any great importance. They may be suctorial or they may be degenerate organs. I consider the stimulus as purely mechanical. The character of the gall may depend upon the location, which would result in difference in tension in different parts of the plant on which the gall may be located and also upon the laws of natural selection, which will be considered in the latter part of this paper.

It would be interesting to know the exact time that cell division begins in the formation of a gall, but it is very difficult to make satisfactory observations upon this point. Adler has made successful observations upon this stage in Neuroterus laviusculus and Biorhiza aptera. He says: "The moment the larva has broken through the egg covering and has for the first time wounded the surrounding cells with its delicate mandibles, a rapid growth begins. This goes on so quickly that while the posterior part of the larva is still within the covering a wall of like growth of cells has already arisen in front. This rapid cell increase can be easily explained because the irritation set up by the emerging larva is exerted upon highly formative cells which collectively possess every condition of growth. The cells which are primarily around the larva cannot be distinguished from the parenchymatous cells from which they proceed."

4. LEPIDOPTERA.

A careful study was made of the mouthparts of the Gelechia solidaginis Fitch (Fig. 111) and upon an undetermined species found upon Rudbeckia laciniata (Part VI). The mandibles are larger and much stronger than in any of the Hymenopterous gallmakers which I examined. The gall is also much stronger than any of the Hymenopterous galls whose larvae were studied. No glandular structures were observed.

CONCLUSION.

1. The fluid secreted by the ovipositor is not an irritant, and therefore cannot be the stimulus for gall production.

2. Since the gall does not form, excepting the Nematus galls, until the appearance of the larvae, it is improbable if oviposition is a stimulus for gall production; and in those insects in which the egg is not deposited within the tissues of the plant it is impossible.

3. Glandular structures were observed in only a few of the Hymenopterous larvae and these were of doubtful character.

4. Since it has so far been impossible to demonstrate the presence of a chemical stimulus except in Nematus, we must consider that the stimulus is usually mechanical. As previously stated (Part I, Conclusion 3) the morphological characters of the gall depend upon the genus of the insect producing it rather than upon the plant upon which it is produced. The early history of all galls except the Cecidomyid is practically the same (Part V, Con. 2). The shape and external character of the gall probably depends upon the following: (1) The plant upon which the attack is made; (2) Upon the part upon which the attack is made; (3) Upon the tissues affected; (4) Upon possible results of natural selection.

SUMMARY OF PARTS.

Next in importance to the problem of a stimulus giving rise to a gall is the explanation of specific external characters. This question is not easily answered and at the present time any explanation must be largely theoretical.

The gall-producing insects are found in six orders, as follows: 1. Arachnida (mites); 2. Hemiptera (Aphidae and Psyllidae); 3. Diptera (Cecidomyidae and Trypetidae); 4. Hymenoptera (Cynipidae and Tenthrenidae); 5. Lepidoptera, and 6, Coleoptera. The gall-producing habit must have originated independently in each of these orders and in some orders (Diptera and Hymenoptera) it must have originated independently in each of the two families represented.

The formation of the gall is due to two primary factors; a stimulus, usually mechanical, given by the insect, and nourishment furnished by the plant.

Conclusions reached as results of previous studies and bearing on this subject are as follows:

1. "Galls may be classified into two general groups, viz.: those produced by mouthparts and those produced by oviposition. Those produced by oviposition may be considered the more highly developed." (Part I, Con. 1.)

2. "The gall does not form until the appearance of the larvae. Therefore all galls are produced by mouthparts." (Part VIII, Con. 1.) The Nematus galls are an exception.

3. "The morphological character of the gall depends upon the genus of the insect producing it rather than upon the plant on which it is produced." (Part I, Con. 3.)

4. "Within each family we find certain morphological resemblances." (Part I, Con. 4.)

5. "The families show parallel lines of development from a low form of gall structure up to a high form." (Part I, Con. 5.)

6. "The presence of at least two zones, of which the inner may be considered nutritive." (Part I, Con. 7.)

7. "The formation of the gall is probably an effort on the part of the plant to protect itself from an injury which is not sufficient to cause death. Both Adler and Fockeu consider that after the first stages of formation the gall becomes an independent organism growing upon the host plant. This is probably true in the highly developed galls of Aphididae, Cecidomyia, and Cynipidae, but the writer is doubtful if this is true in the less complex galls of Acarina, Aphididae and Cecidomyia." (Part I, Con. 8 and Part V, Con. 6.)

8. "In the formation of all leaf galls except the Cecidomyia galls the normal cell structure of the leaf is first modified by the formation of a large number of small, compact, irregularly shaped cells. In the galls of Acarina and Aphididae this is followed by a development of trichomes, especially in the former. In all galls the mesophyll is subject to the greatest modification. Many small fibro-vascular bundles are formed in this modified mesophyll." (Part V, Con. 2.)

9. "Trichomes are far more common in galls produced by mouthparts than in those produced by oviposition." (Part V, Con. 9, and see Summary 2.)

10. "Variation in galls is due to their being produced by insects of different orders, to their working upon different parts of the plant and upon different tissues of these parts." (Part III, Con., and Part IV, Con. 1.)

I. ARACHNIDA.

The Arachnida galls are of four types: (1) A modification in the epidermis of the leaf as in the Phytoptus galls on maple and elm; (2) A fold in the plant tissue causing a cavity filled with trichomes, among which the parasites live, as in the case of many Phytoptidi (Figs. 8, 9, 10, 11, 43, 44, 45, Parts I and V); (3) A swelling with an exposed surface covered with trichomes, among which the parasites live, as in the case of Erineum

anomalum (Part V, Figs. 47, 48); (4) The witchbroom formation, as in the case of the Phytoptus sp——, and Sphaerotheca phytoptophila Kell. and Sw. on Celtis occidentalis.

The author has studied only the second and third types. The difference between these two may be accounted for by the fact that the Phytoptus attacks the blade while the Erineum attacks the petiole, mid-rib or larger vein. The part affected undergoes a curvature in each case in the direction of the least resistance.

2. HEMIPTERA.

The method of attack by the Hemiptera is practically the same as in Arachnida, i. e., by sucking mouthparts. The galls present a complete serial line of development, the lowest form being a simple curling of the leaf as in the case of Schizoneura americana, the next higher, a simple folding of the leaf, as in the case of Colopha ulmicola, the next higher is a more complex structure, such as the Phylloxera galls and H. hamamelis, the next higher, the slightly more complex, as in the case of the Pemphigus galls (Figs. 12 to 21, and 49 to 58). The galls of the Pachypsylla (Figs. 59, 60) are the most highly developed of the entire series.

Although in this case we have a complete series, it is difficult to understand how this development has been produced. It may be that the different forms are due to the attack being made upon different tissues in each case, or to the degree in which the tissues are injured. Upon this point we have no direct proof. However, there is very little doubt that the stimulus is entirely mechanical.

3. DIPTERA.

As previously stated, the Cecidomyid galls are far more varied in location and in morphological structure than any other group of galls and show less number of characters peculiar to themselves alone. There is not sufficient data to draw even theoretical conclusions concerning the influencing causes in their development.

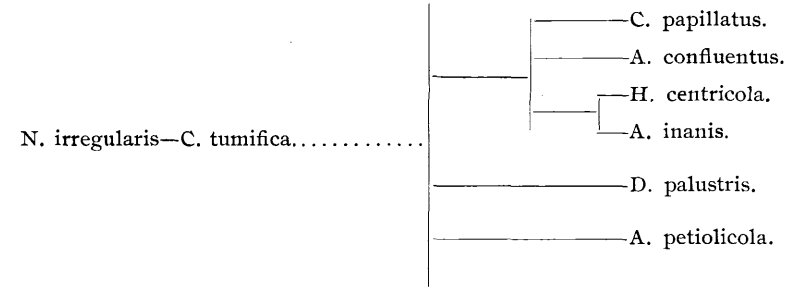
4. HYMENOPTERA.

As previously stated, the Cynipidous galls are the most highly developed and show a greater number of morphological structures peculiar to themselves than any other group (Part I, Con. 2; Part V, Con 3).

Since the gall does not begin to develop until after the hatching of the larvae, oviposition cannot be an important factor except in so far as it is necessary to have the egg placed in certain tissues.

Examination of the mouthparts show few, small and insignificant gland-like structures the character of which is doubtful. It is therefore probable that the stimulus is purely mechanical except in the Nematus. But how are we to account for the great num-

ber of specific external characters? Let us first review the structural characters of the leaf galls, since these galls show the most uniform line of development. Considering Neuroterous irregularis the gall of greatest simplicity, we can formulate the following diagram:



In N. irregularis the zones are not so well developed as in C. tumifica. In C. tumifica the zones are perfect, but in contact. In C. papillatus the protective and parenchyma zones are separated, but connected by long parenchyma cells. In H. centricola and A. inanis the protective and parenchyma zones are connected by fibro-vascular bundles. In A. confluentus they are connected both by fibro-vascular bundles and by parenchyma cells (Fig. 121). In D. palustris the parenchyma and protective zones are not connected. In A. petiolicola the zones are in contact, but the tissues are very dense, due to location in the petiole of midrib of the leaf.

If galls become independent structures they are undoubtedly subject to the same laws of natural selection as any other group of organisms, or if they be considered as parts of the plant they must also be subject to the same laws of natural selection as any other part of the plant on which they live. How, then, have these laws affected the gall? It may be a protective coloration against birds and rodents, and other insects, but this cannot be very important since many species of galls are very conspicuous. Furthermore, animals make but very little use of galls for food. So far I have observed other animals using galls for food but once and then birds were tearing open the large galls of Pemphigus vagabundus and eating the insects. The tannin which develops in such abundance in all galls as they approach maturity is probably a great protection against insectivorous animals.

The greatest insect enemy with which the gall insect has to contend is the great number of parasites. The size, shape and character of the epidermal covering of the gall may be a protection against this numerous enemy. The thickness of the gall and the density of the tissues, especially the protective zone, is an

important protective device. The large intercellular chambers in the parenchyma zone place the larvae at a great distance from the surface of the gall without increasing the amount of work necessary for the mature insects to accomplish before reaching the outside; this is undoubtedly a great protection against parasites, since it increases the difficulties for the parasite in reaching the larvae with the ovipositor, The development of these protective devices is probably the result of natural selection. Since the character of the gall depends upon the insect, many variations in the gall may also depend on variations in the stimuli given by the insect. If these variations in character of epidermis, in thickness of parenchyma zone, in the formation of large intercellular spaces, in thickness and density of protective zone, are advantageous to the insect in protecting it from the numerous parasites, these characters may be perpetuated in succeeding generations and the gall may increase in complexity. Natural selection is a reasonable explanation.

It should be remembered that the plant is making an effort to resist a parasite from which it cannot escape. The gall-maker derives its nourishment without destroying its host and at the same time strives to protect itself as far as possible from the great number of parasitic enemies. The food supply first becomes a part of the gall and upon this supply which, in the case of the Cynipidae, is stored in the nutritive zone, it feeds.

Any irritation, such as the cutting or puncturing of plant tissues, may and usually does cause excessive growth. It is probable that the primitive galls were of a type similar to the simplest of the Phytoptus galls, i. e., a peculiar growth of the epidermal cells. The next step in the evolution of the gall may be represented by a type similar to Schizoneura americana, in which case the stimulus is greater, resulting in a curling of the leaf. The next step may be represented by a type similar to the more complex Phytoptus galls, H. hamamelis, C. ulmicola, the Phylloxera, the Pemphigus and the most complex of the Pachypsylla galls in which we find a series of more or less complex folds in the leaf up to the increase in amount and differentiation of the tissue as in the case of P. p.-mamma.

In the Cynipidous galls we have the greatest complexity, but also a factor somewhat different from that in the forms to which we have referred, i. e., the placing of the egg below the surface and in those tissues upon which the larva is expected to feed. It is impossible to say whether this habit of placing the egg below the surface was acquired before or after the gall-making habit, but it must be a great advantage to the insect. These galls, as previously demonstrated, show the more complex serial line of development of any of the galls, but even the simplest of these is more complex than the most complex gall produced by any other

order of insect. This very complex development is due to an early acquirement of the gall-making habit or to more rapid evolutionary development as a result of the deposition of the egg below the surface.

The greater part of the work connected with Part IX of this series was conducted at the Lake Laboratory of the Ohio State University at Sandusky, Ohio, and I am very much indebted to the Director, Professor Herbert Osborn, for valuable assistance. I also wish to express my thanks to the many friends who have collected material and otherwise aided in these studies.

This series of papers will be presented to the Faculty of the College of Arts, Philosophy and Science, of the Ohio State University, as the thesis requirement for the degree of Doctor of Philosophy, June, 1904.

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EXPLANATION OF PLATES IX–XII.

The drawings were made with a Bausch & Lomb microscope. For Figs. 70–76 and Figs. 84–91 and Fig. 93b, a Number 2 ocular and 1/6 objective. For Figs. 77–83, a Number 2 ocular and 1/12 immersion objective. With Figs. 92–98 and Figs. 106a, 110 and 111, a 3/4 ocular and 2/3 objective. For Fig. 93 a Number 2 ocular and 2/3 objective. The reduction is not so great as in the preceding parts and therefore the figures are proportionately slightly larger. The diagrams were not made upon a definite scale. The numbering of the drawings is continuous with the preceding parts.

Abbreviations: e. epidermis. nu.—nutritive zone.
ep.—epidermal zone. f. v. b.—fibro-vascular bundles.
pa.—parenchyma zone. l. c.—larval chambers.
p.—protective zone. sc.—sclerenchyma.

FLOWER AND FRUIT GALLS.

70. Section of leaf of Euphorbia corollata.
71a. Diagram of section of Phytoptus sp—— gall on leaf of E. corollata.
71b. Section of 71a.
72a. Section of lower part of ovary of E. corollata affected by Phytoptus sp——.

72b. Section of upper part of flower of E. corollata affected by Phytoptus sp——.
73a. Diagram of cross section of Cecidomyid bud gall on Solidago canadense.
73b. Section of same.
74a. Diagram of longitudinal section of Cecidomyid gall on Ratibida pinnata.
74b. Diagram of longitudinal section of Cecidomyid gall on Ratibida pinnata.
74c. Section of 74b.
75a. Section of unaffected fruit of Prunus virginiana.
75b. Section of Cecidomyid gall developed in fruit of P. virginiana.

ROOT GALL.

76a. Section of young gall of Amphibolips radicola.
76b. Section of mature gall of A. radicola.

HISTOLOGY.

77. Section of young gall of Phytoptus quadripes.
78. Section of young gall of Phytoptus abnormis.
79. Section of nutritive zone of young gall of Amphibolips inanis.
80. Section of mature gall of A. inanis.
81. Section of mature gall of Callirhytis papillatus. (Nutritive, protective and part of parenchyma zones.)
82. Section of mature gall of Dryophanta palustris. (Nutritive, protective and part of parenchyma zones.)
83. Section of mature gall of Andricus petiolicola.

SURFACE SECTIONS OF

84. Dryophanta palustris. (Very young gall.)
84b. Dryophanta palustris. (Mature gall.)
85. Amphibolips inanis.
86. Diastrophus siminis.
87. Diastrophus potentilla.
88. Pachypsylla c.-mamma.
89. Colopha ulmicola.
90. Phylloxera c.-globuli.
91. Pemphigus p.-transversus.

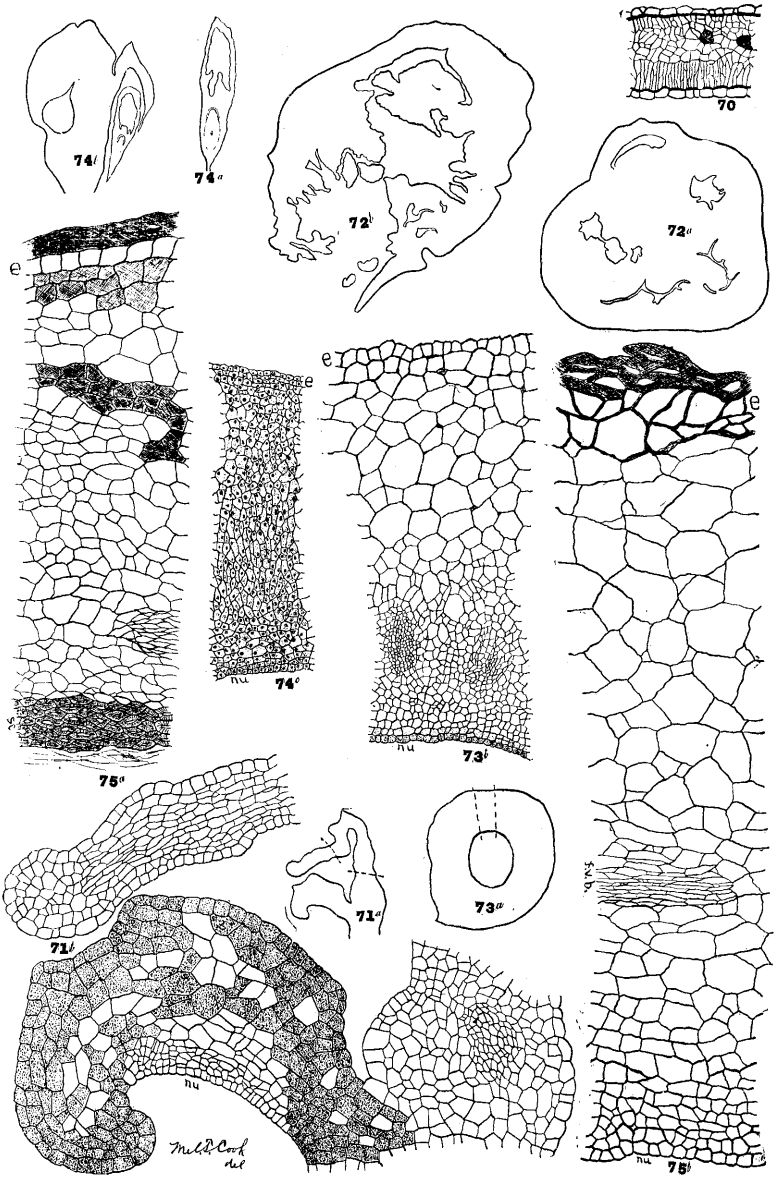
OVIPOSITORS OF

92. Cecidomyia gleditsiae.
93a. Nematus salicis-ovum.
93b. Nematus salicis-ovum.
94. Dryophanta palustris.
95. Amphibolips radicola.
96. Andricus cornigerus.
97. Andricus seminator.
98a. Rhodites radicum.
98b. Rhodites radicum.

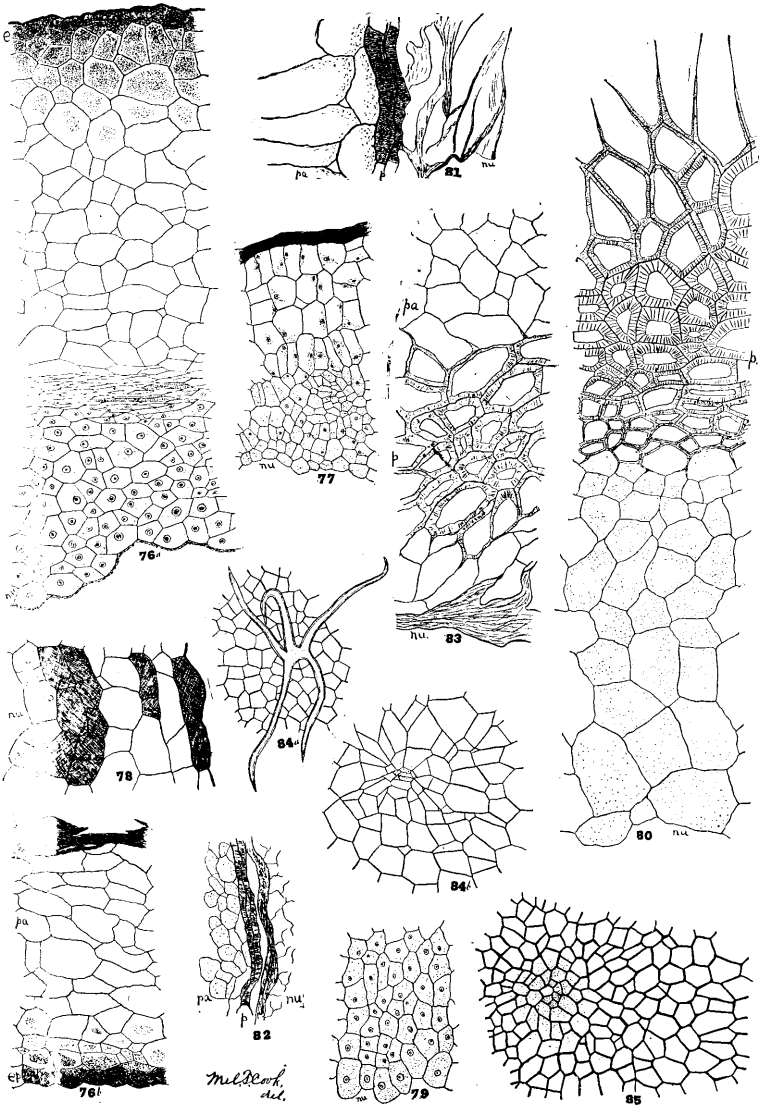
MOUTHPARTS OF

99. Colopha ulmicola.
100a. Pachypsylla c.-mamma, with setae extended.
100b. Pachypsylla c -mamma, with setae retracted.
101. Cecidomyia gleditsiae.
102. Cecidomyia pellex.
103. Andricus petiolicola.
104. Amphibolips inanis.
105. Amphibolips confluentus.
106a. Diastrophus siminis.
106b. Diastrophus siminis.
107. Callirhytis papillatus.
108. Parasite from gall of C. papillatus.
109. Holcaspis globulus.
110. Nematus pomum.
111. Gelechia gallae-solidaginis.

OHIO NATURALIST. *Plate IX.*



COOK on "Galls and Insects Producing Them."



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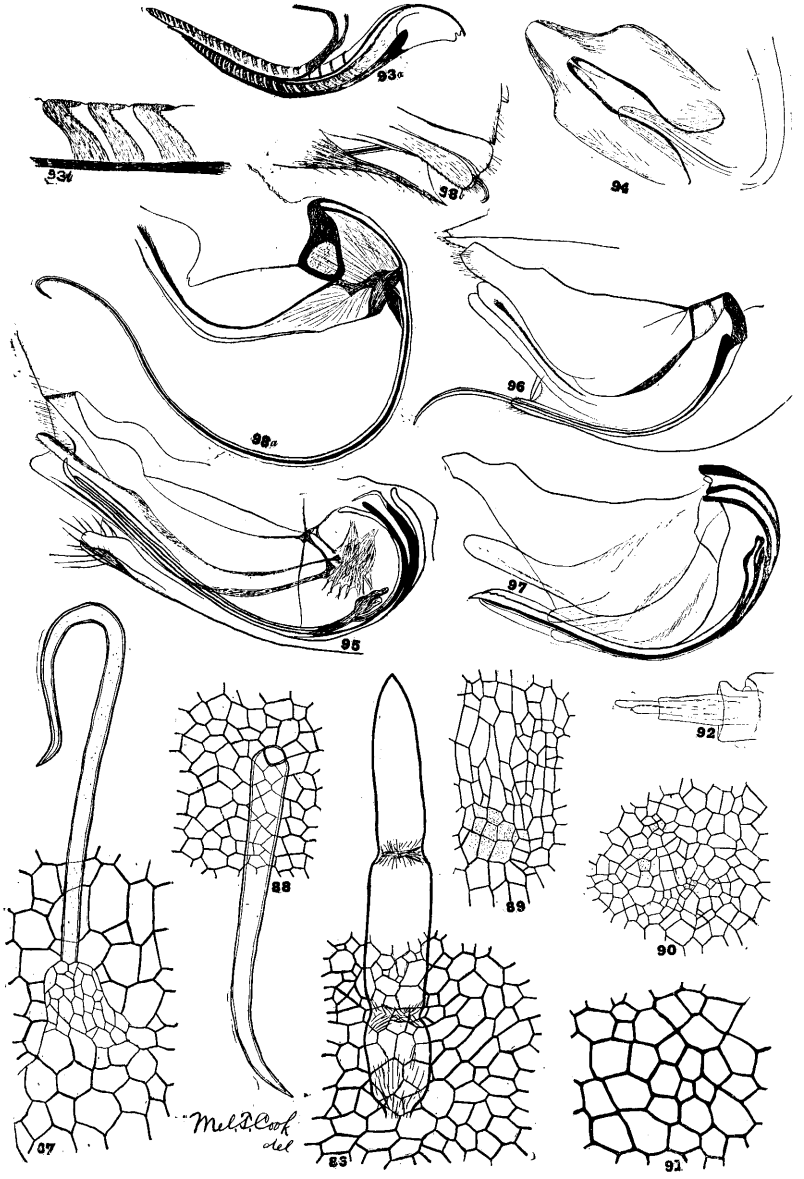
OHIO NATURALIST. *Plate XI.*



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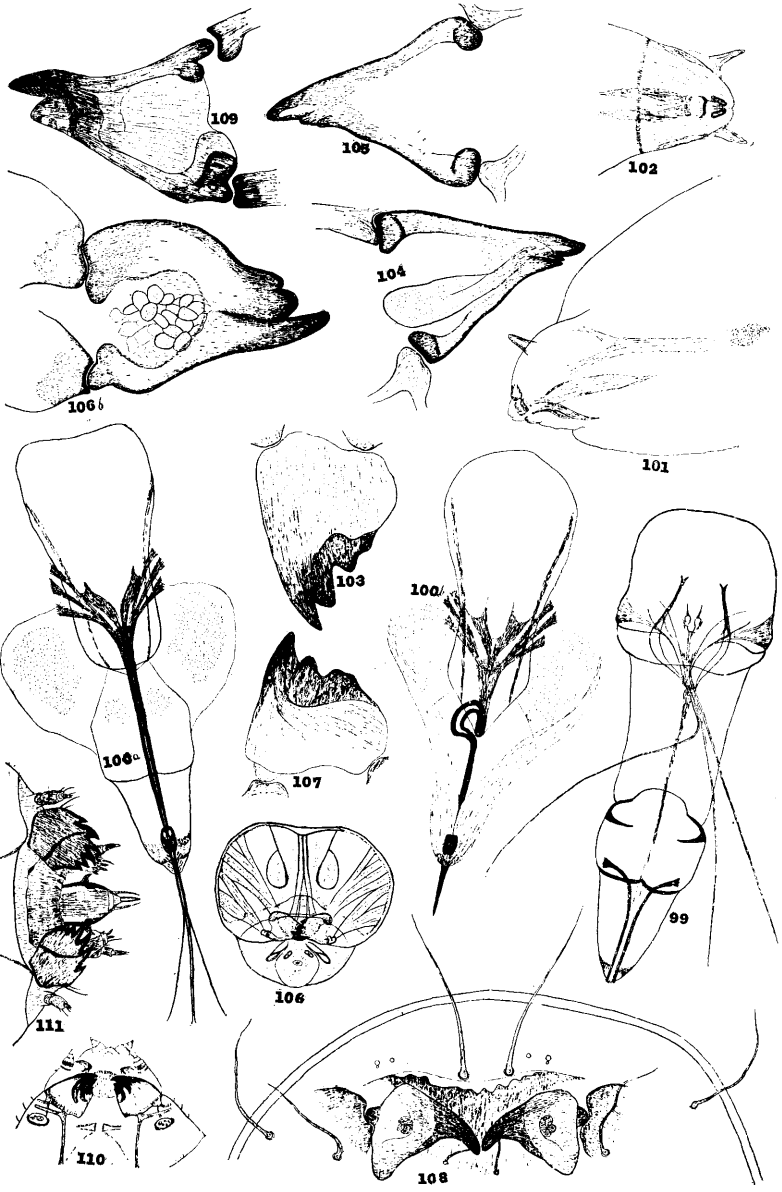

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